

Mining biodiversity databases establishes a global baseline of cosmopolitan Insecta mOTUs: a case study on Platygastroidea (Hymenoptera) with consequences for biological control programs

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Abstract

In the past decade, several species of platygastroid wasps were found to be adventive in North America and Europe while under evaluation in quarantine as biological control agents of invasive pests. The scope and relative risk of this phenomenon is not fully known, but it is clearly a trend with implications for classical biological control. As a means of assessing the issue and to provide a global baseline, we implemented a data-mining approach with DNA sequences in the Barcode of Life Database, yielding 201 platygastroid BINs with intercontinental and island distributions. At least fifty-five BINs displayed exact COI barcode matches across continents, with many more BINs scored as inconclusive due to sequence length variation. These intercontinental and island BINs include biocontrol agents known to be adventive, as well as many species identified only to genus with uncertain geographic origins. We provide 2,500 identifications for platygastroid BOLD BINs, 88% to genus, to encourage additional research on this distributional phenomenon. The intercontinental BOLD BINs were compared to literature records and GBIF occurrences of cosmopolitan species to identify gaps and discordance across data sources. Smaller COI barcode datasets from localities in Florida and Germany, including topotypical specimens, revealed more intercontinental matches. We analyzed COI sequences in BOLD for the entirety of Insecta and Araneae to assess

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this phenomenon more broadly and because these taxa contain many hosts for platygastroid wasps. This method revealed that the intercontinental distribution phenomenon is widespread with implications for assessing biological diversity, taxonomic methodology and regulatory frameworks.

Keywords

adventive species, biological control, biodiversity databases, COI barcoding

Introduction

Human-mediated movement of insect pests is a well-known phenomenon, and mitigation attempts often include classical biological control. Relatively recent invasive stink bugs (Hemiptera, Pentatomoidea) in the United States include the kudzu bug (Megacopta cribraria Fab.), the brown marmorated stink bug (Halyomorpha halys (Stål)) and bagrada bug (Bagrada hilaris Burmeister); management efforts for all of them included classical biological control using egg parasitoids in the family Scelionidae (Hymenoptera, Platygastroidea). In each case, the biological control agent in quarantine was found to be adventive prior to approved release, circumventing regulatory processes and establishing expanded geographic ranges without oversight (Gardner et al. 2013; Talamas et al. 2015; Milnes et al. 2016; Ganjisaffar et al. 2018; Servick 2018; Hogg et al. 2021; Talamas et al. 2021). In the case of Trissolcus japonicus (Ashmead) attacking H. halys, this resulted in an immediate shift from determining if the parasitoids could be released, to tracking their movement and ecological effect (Buffington et al. 2018). This phenomenon, in which parasitoids are found in association with recently adventive pests, has been documented in Mexico, Chile and throughout Europe (Sabbatini-Peverieri et al. 2018; Lomeli-Flores et al. 2019; Stahl et al. 2019; Rojas-Gálvez et al. 2021; Dieckhoff et al. 2021) and is not limited to biological control agents that are waiting to be deliberately introduced. In the United States, two species that parasitize stink bug eggs, *Psix tunetanus* and *Ps. striaticeps*, are known to be adventive (Johnson and Masner 1985; Birkmire et al. 2021), but were not imported into quarantine as part of a biological control program.

The prevalence of unintended introductions remains largely unevaluated and the numerous detections of scelionid parasitoids of stink bugs is probably a reflection of the attention given to these organisms. DeBach and Rosen (1991) estimated that forty-three percent of exotic beneficial arthropods in the United States arrived by accident. Sporadic appearance of biological control agents targeting invasive pests in new environments may be considered "fortuitous" (DeBach 1971). However, by definition, the consequences for native, non-target organisms remain unknown pending post hoc analysis. Tabulating the number of unintentionally introduced platygastroid wasps is even more problematic. An accurate estimate may be impossible to generate at present because taxonomic preparedness (Wheeler and Cracraft 1997) is generally lacking in hyper-diverse, economically important insect groups. Popovici et al. (2018) documented 'tramp' species in three platygastroid genera, all of which were identified

morphologically. This approach requires intimate knowledge of the world fauna and access to a cosmopolitan representation of specimens. Even when unintended introductions are detected relatively quickly (e.g., *Trissolcus japonicus*), verification of the species identity may require significant research and most cases are unlikely to be investigated extensively. As of 2021, twenty-nine platygastroid wasp species were considered introduced or invasive in the United States (Simpson et al. 2021) and we consider this to be an underestimate based on recent research (Talamas et al. 2021; Birkmire et al. 2021). Only eight introduced platygastroid species are documented in Europe and three of these were deliberate releases (Katsanevakis et al. 2015).

We suspect that unintended introductions of platygastroids will be increasingly detected as 'dark taxa' (Page 2016) in sequencing databases. The aptly named Gryon aetherium Talamas (Talamas et al. 2021) perfectly illustrates an instance where the range expansion of a 'dark taxon' was first detected by COI barcode matches and its classification and taxonomy were established subsequently. Gryon aetherium is a parasitoid of the pestiferous Bagrada bug (B. hilaris), which is found from South Africa to India. Given the size of this geographic range, hundreds of Gryon holotype specimens and descriptions had to be examined in detail before the species could be confidently described as new. The urgency increased as adventive populations were found in both North and South America and it was only with years of preceding work that the adventive populations in the United States and Chile could be reported with a species name - concurrent with the description of G. aetherium (Lomeli-Flores et al. 2019; Hogg et al. 2021; Rojas-Gálvez et al. 2021; Talamas et al. 2021). The potential for sequence databases to reveal adventive arthropod populations is significant, but limited by the metadata and level of identification associated with the sequences. For Platygastroidea, the Barcode of Life Database (BOLD; Ratnasingham and Hebert (2007)) contains nearly 140,000 scelionid and platygastrid sequence records as of October 2022. Most of these were bulk-sequenced as part of national initiatives and did not receive thorough taxonomic treatments. A total of 128,000 of these BOLD records are unidentified at the species level, whereas 108,000 are unidentified at the genus level. Accordingly, the number of platygastroid dark taxa potentially present in BOLD is staggering and association with existing names by comparison to type material, made by expert taxonomists, is a gigantic scientific effort.

In this contribution, we employed multiple research tracks to address the question of how many species of Platygastroidea may be moving over intercontinental distances while eluding detection. (1) We used existing BOLD infrastructure to identify platygastroid BINs (Barcode Index Numbers; database calculated clusters of highly similar sequences used to approximate species) that spanned large geographic areas. (2) Intercontinental platygastroid BINS were identified to genus. To ameliorate taxonomic impediments in the database and facilitate future research, we identified one fifth of all platygastroid BINs in BOLD to genus. (3) For each platygastroid genus with an intercontinental BIN, we compared the results of our data-mining approach with distributional data from taxonomic literature and the Global Biodiversity Information Facility (GBIF). (4) We incorporated data from two geographically disparate COI barcoding

projects that share the goal of reliably attaching species names to DNA sequences. The first was a year-long insect trapping effort in Jacksonville, Florida, USA, a type locality for many platygastroids described at the turn of the 20th century. Importantly, traps were operated near the Port of Jacksonville, a potential site of entry for exotic species. The second was the German Barcode of Life III: Dark Taxa, which seeks to enhance the size and quality of the German DNA barcode reference library and includes collecting localities from which platygastroids were described in the 19th century. By generating COI barcodes from topotypical specimens and comparing these specimens to primary types as part of the identification, we made the most reliable association possible between a DNA sequence and a historical name, apart from using DNA from primary types directly. Additionally, this is the most feasible means to infer directionality of movement for species that appear to have adventive distributions. (5) We implemented our data-mining protocol for Insecta and Araneae for two reasons. First, platygastroids parasitize a taxonomically diverse array of insect and spider hosts and data about their distributions might inform our results for Platygastroidea. Second, the phenomenon of intercontinental distributions of arthropods more broadly is worthy of attention, and we sought to demonstrate the scalability of our approach.

Materials and methods

BOLD data-mining for Platygastroidea

Beginning in October 2022, BOLD v.4 (Ratnasingham and Hebert 2007) was manually datamined for Platygastroidea BINs with intercontinental distributions. Our search terms for Platygastroidea followed the revised classification of Chen et al. (2021), which recognized Geoscelionidae, Janzenellidae, Neuroscelionidae, Nixoniidae, Platygastridae, Scelionidae and Sparasionidae as the extant families. The BOLD BIN database portal was queried with the following family and genus level terms: "Geoscelionidae", "Janzenellidae", "Neuroscelionidae", "Nixoniidae", "Platygastridae", "Scelionidae", "Sparasionidae", "Huddlestonium", "Plaumannion", "Janzenella", "Neuroscelio", "Nixonia", "Archaeoteleia", "Mexon", "Listron", "Sceliomorpha" and "Sparasion". The resulting BINs were then assessed for the number of countries in which they occurred. BINs with multiple countries were further scrutinized. If the countries were on different continents or otherwise spanned large distances (e.g., Pacific islands and the mainland), then the BIN was included in the dataset. A set of information was recorded and downloaded for each intercontinental BIN: BOLD BIN, BOLD taxonomy lowest level, maximum intra-BIN p-distance, distance to nearest neighbor BIN, the BIN fasta file of COI sequences and the Darwin Core (Wieczorek et al. 2012) BIN metadata text file (10.5281/zenodo.7930011; 10.5281/zenodo.7930274).

In February 2023, the dataset was expanded using an automated scripting approach (10.5281/zenodo.7930407). The Darwin Core data files for "Insecta" and "Araneae" were downloaded from BOLD. The Insecta files were downloaded on 3 January 2023.

The Araneae files were downloaded on 16 March 2023. The Insecta file was examined for all the categories listed under the field "country". The country fields were assigned to continents or island categories (Suppl. material 1). Continent assignments largely followed the United Nations Statistics Division (2023) designations, except in a few edge cases where changes were made to follow the borders of zoogeographic regions more closely. Edge cases were assigned to groups based upon the closest alignment of political boundaries and biogeographical barriers. To separate the Asian and European continents, Russia was divided along provincial borders that most closely continue the line of the Ural Mountains southward. Turkey, Georgia, Armenia and Azerbaijan were included in Europe to avoid dividing the Caucasus region. Island nations sufficiently distant from continents were placed into four categories based on oceanic region. The Indonesian provinces of Papua and West Papua were included in the Australian region to avoid dividing the island of New Guinea. Solomon Islands, New Caledonia and New Zealand were grouped with Australia.

DNA sequence alignment, tree building and match scoring

Each BIN in the intercontinental and island platygastroid dataset was individually analyzed to determine whether they contained exact COI barcode matches across large distances. Each BIN's COI fasta file was aligned using the default settings of MUSCLE (Edgar 2004) as implemented in MEGA7 (Kumar et al. 2016). In MEGA7, these individual BIN alignments were used to build neighbor-joining trees (when there were more than two terminal taxa) and distance matrices. Analysis settings were identical for both approaches: the data were labelled as protein-coding nucleotide sequences with the invertebrate mitochondrial genetic code, p-distance set as the method/model, substitutions included transitions and transversions, rates among sites were uniform and missing data treatment was set to partial deletion with a 95 percent site coverage cutoff. P-distance calculations involving > 255 terminal taxa were exported as matrices. P-distance calculations involving > 255 terminal taxa were exported as pairwise columns. Neighbor-joining trees were exported as Newick tree files and uploaded into the online annotation portal of Interactive Tree of Life (iTOL) v.5 (Letunic and Bork 2021).

Trees were viewed in iTOL to determine individual sequence membership in haplotype clusters. Apparent haplotype matches were then examined in the p-distance calculation files for confirmation. The geographic distribution of exact matches was evaluated by examining the specimen level metadata present in the BIN's Darwin Core text file. Putative exact intercontinental matches were then validated in the underlying DNA alignment. This was necessary due to slight variation in the length of COI barcode sequences. If longer sequences in the alignments displayed polymorphisms toward either the 5' or 3' ends and the putative intercontinental matches lacked these flanking data, then the matches were considered inconclusive. Ambiguous DNA base pairs were ignored for considering exact matches.

Individual BIN alignments were ultimately combined into one fasta file for tree building and visualization. A species of *Periclistus* Förster (Hymenoptera, Proctotrupomorpha,

Cynipidae) with appropriate data coverage was selected to root subsequent analyses, based on the sister relationship of Cynipoidea to Platygastroidea (Blaimer et al. 2023). Alignment of the combined intercontinental and island COI barcode dataset was performed in the MAFFT online service v.7 (Katoh et al. 2019) with the FFT-NS-1 setting. This alignment (Suppl. material 3) was used for neighbor-joining analysis in MEGA11 (Tamura et al. 2021) using the same tree building parameters described above. This tree topology (Suppl. material 4) was manipulated for viewing ease and annotated in iTOL v.5 (Letunic and Bork 2021) and FigTree v.1.4.4 (Rambaut 2018) (Suppl. material 5).

Identification and BOLD digital morphology

During the above data-mining activity, it was noticed that a large proportion of plat-ygastroid BINs were unidentified below the family level. A list of Platygastroidea BINs was pulled from BOLD as candidates for identification using the provided digital morphology framework. Identifications were made, when possible, by comparison to images of primary type specimens provided by Talamas et al. (2017). Most Platygastroidea BINs were sight-identified using the BOLD BIN images to family, sub-family, tribe or genus by taxonomic specialists Elijah Talamas, Zachary Lahey and Jessica Awad.

GBIF data-mining and literature search

Genus level occurrence data (Table 1) were downloaded as Darwin Core Archives from the Global Biodiversity Information Facility (GBIF 2022) for all platygastroid genera identified in the intercontinental BIN dataset. These occurrence data were sorted by species, then country, to determine which species had records from more than one continent (Suppl. material 6). Relevant taxonomic revisions were searched to corroborate intercontinental taxa reported in GBIF and BOLD. For a total evidence analysis of Platygastroidea, the GBIF, literature and BOLD datasets were combined to assess their continental and island connections. Species with records from multiple data types were only counted once and their geographic occurrences were rectified for analysis.

Field work

Topotypes of platygastroid species described from Duval County, Florida, were collected between July 2018 and December 2021 in and around the Timucuan Ecological and Historic Preserve near the mouth of the St. Johns River. These collections were largely from Malaise traps that were placed at three different sites in the area. Collecting heads were provisioned with propylene glycol and wrapped with aluminum foil to prevent UV damage to the specimens. 3D printed yellow cylinder traps were experimentally deployed on the ground and suspended from overhanging branches during one sampling period and additional specimens were collected in yellow pan traps and by sweep netting around the trap sites. Bulk samples were returned to the laboratory and sorted under a Zeiss Discovery V8 Stereomicroscope. All platygastroid specimens were transferred to 95% ethanol and screened for matches to species described from that area.

Table 1. GBIF occurrence datasets used for comparison with the intercontinental BINs.

Family	Genus	GBIF Occurrence Dataset Citation
Platygastridae	Allotropa	GBIF.org (31 October 2022) GBIF Occurrence Download
		https://doi.org/10.15468/dl.n3derh
Platygastridae	Amitus	GBIF.org (31 October 2022) GBIF Occurrence Download
		https://doi.org/10.15468/dl.xjcn95
Platygastridae	Amblyaspis	GBIF.org (28 October 2022) GBIF Occurrence Download
		https://doi.org/10.15468/dl.r8zptf
Platygastridae	Aphanomerus	GBIF.org (28 October 2022) GBIF Occurrence Download
		https://doi.org/10.15468/dl.gw43u4
Platygastridae	Euxestonotus	GBIF.org (28 October 2022) GBIF Occurrence Download
		https://doi.org/10.15468/dl.gu7djg
Platygastridae	Fidiobia	GBIF.org (14 February 2023) GBIF Occurrence Download
		https://doi.org/10.15468/dl.w478bm
Platygastridae	Leptacis	GBIF.org (31 October 2022) GBIF Occurrence Download
		https://doi.org/10.15468/dl.efh6t8
Platygastridae	Metaclisis	GBIF.org (31 October 2022) GBIF Occurrence Download
		https://doi.org/10.15468/dl.qjwpf5
Platygastridae	Platygaster	GBIF.org (31 October 2022) GBIF Occurrence Download
		https://doi.org/10.15468/dl.d7n4wt
Platygastridae	Synopeas	GBIF.org (31 October 2022) GBIF Occurrence Download
		https://doi.org/10.15468/dl.ev6apy
Scelionidae	Anteris	GBIF.org (31 October 2022) GBIF Occurrence Download
		https://doi.org/10.15468/dl.sjsua4
Scelionidae	Aradophagus	GBIF.org (31 October 2022) GBIF Occurrence Download
		https://doi.org/10.15468/dl.hbu7rt
Scelionidae	Baeoneurella	GBIF.org (31 October 2022) GBIF Occurrence Download
		https://doi.org/10.15468/dl.dw6d4e
Scelionidae	Baeus	GBIF.org (31 October 2022) GBIF Occurrence Download
		https://doi.org/10.15468/dl.9hxwkx
Scelionidae	Baryconus	GBIF.org (31 October 2022) GBIF Occurrence Download
		https://doi.org/10.15468/dl.qaraf2
Scelionidae	Calliscelio	GBIF.org (15 February 2023) GBIF Occurrence Download
		https://doi.org/10.15468/dl.bsua2e
Scelionidae	Dicroscelio	GBIF.org (31 October 2022) GBIF Occurrence Download
		https://doi.org/10.15468/dl.67g54v
Scelionidae	Dyscritobaeus	GBIF.org (20 February 2023) GBIF Occurrence Download
		https://doi.org/10.15468/dl.5mt6wa
Scelionidae	Gryon	GBIF.org (31 October 2022) GBIF Occurrence Download
		https://doi.org/10.15468/dl.tn8kne
Scelionidae	Hadronotus	GBIF.org (31 October 2022) GBIF Occurrence Download
		https://doi.org/10.15468/dl.9qz232
Scelionidae	Idris	GBIF.org (31 October 2022) GBIF Occurrence Download
		https://doi.org/10.15468/dl.h2qj4j
Scelionidae	Platyscelio	GBIF.org (13 December 2022) GBIF Occurrence Download
		https://doi.org/10.15468/dl.cprkz3
Scelionidae	Psix	GBIF.org (31 October 2022) GBIF Occurrence Download
		https://doi.org/10.15468/dl.cc9rkg
Scelionidae	Telenomus	GBIF.org (31 October 2022) GBIF Occurrence Download
		https://doi.org/10.15468/dl.32xjmc
Scelionidae	Trimorus	GBIF.org (31 October 2022) GBIF Occurrence Download
		https://doi.org/10.15468/dl.ytcg37
Scelionidae	Trissolcus	GBIF.org (31 October 2022) GBIF Occurrence Download
		https://doi.org/10.15468/dl.t4qbu5
Scelionidae	Xenomerus	GBIF.org (31 October 2022) GBIF Occurrence Download
		https://doi.org/10.15468/dl.5vzkr6

COI barcoding of Florida specimens

DNA was non-destructively extracted from specimens using the Qiagen DNeasy Blood and Tissue Kit. Molecular voucher specimens were recovered and deposited at the Florida State Collection of Arthropods (Florida Department of Agriculture and Consumer Services – Division of Plant Industry; Gainesville, Florida). PCRs were conducted as 25 µl reactions using the KAPA HiFi HotStart Readymix Kit (Roche Diagnostics) per the manufacturer's recommended protocol. Oligonucleotide primers used for PCR and direct sequencing were the universal arthropod COI barcoding sets LCO1490/HCO2198 (Folmer et al. 1994) and LEP-F1/LEP-R1 (Hebert et al. 2004). PCR products were visually verified by gel electrophoresis and positive products were prepared for sequencing with the Qiagen QIAquick PCR purification kit. PCR products were bidirectionally sequenced utilizing BigDye Terminator v.3.1 chemistry on the Applied Biosystems SeqStudio platform. Sequence traces were trimmed and assembled into contigs in Sequencher 5.4.8 and Geneious Prime. New COI barcodes were uploaded to BOLD and GenBank (OQ561913–OQ561961) and assessed for their nearest matches.

COI barcoding of German specimens

The German Barcode of Life III: Dark Taxa project (Hausmann et al. 2020) provided 34 platygastrine specimens matching 14 BINs with intercontinental distributions. These were selected for closer morphological examination and taxonomic analysis. Methods for trapping, non-destructive DNA extraction and COI sequencing follow Awad et al. (2021). Species partitioning was performed with ASAP (Puillandre et al. 2021) using the Jukes-Cantor model and default web server settings.

Photography

Following non-destructive DNA extraction, voucher specimens were mounted and photographed with a Macropod imaging system consisting of a Canon EOS 6D Mark II camera body, EF 70–200 mm lens and 10× or 20× M Plan APO Mitutoyo objective lenses. Imaging software included Canon EOS Utility 3.14.30.4 and Helicon Focus Pro 7.7.5 for image stacking. Adobe Photoshop 23.2.2 was used for limited post-processing and addition of scale bars. Images were uploaded to BOLD with specimen metadata.

BOLD data-mining for Insecta and Araneae

An R (R Core Team 2022) script was developed that created two outputs: 1) a list of BINs with intercontinental or mainland/island distributions and their associated metadata (e.g., taxonomic information) and 2) a list of BINs with intercontinental or mainland/island distributions and an individualized tally of long-distance occurrences. The platygastroid data were compared to our manually-extracted list. The taxonomic

spread in the Insecta file was summarized at the family and genus level, with special attention given to known host groups for platygastroids. Summary statistics were completed with R 4.2.2 (R Core Team 2022), using the dplyr (v.1.0.10; Wickham et al. (2022)), data.table (v.1.14.8; Dowle and Srinivasan (2023)), and stringr (v.1.4.1; Wickham (2022)) data manipulation packages. Data was visualized using the package ggplot2 (v.3.4.1; Wickham (2016)). The full reproducible code is available in Supplementary materials (10.5281/zenodo.8380145).

A randomized 5% of the recovered Insecta and Araneae BINs were validated by manual examination in the BOLD BIN database (Suppl. materials 2, 19). Only the first page of returned search results (which contain order, species and country level distribution) were examined in the validation process. BINs with many different species identifications were scored as having minor taxonomic conflicts. BINs with multiple species or genus identifications were scored as having major taxonomic conflicts, except when it appeared that specific epithet discrepancies were due to varying genus classifications. The list of recovered Insecta and Araneae BINs was summarized at the family and genus level. BINs containing known host groups of Platygastroidea were similarly summarized. The Insecta and Platygastroidea occurrence datasets were transformed into pairwise matrices capturing their geographic distributions. Matrices (Suppl. materials 10, 12–16) were imported to the online version of Circos (Kryzwinski et al. 2009) for visualization. Default settings were used in the online Circos viewer with the exception of the following: 1) labels segment set to large, 2) data filters intra-segment cells hidden, 3) row and column segments order set to col/row ratio, 4) row and column segments with normalized segment size set to remap segments size to 1000, 5) contribution tracks set to hide and no stroke, 6) ribbon caps completely disabled, 7) ratio layout enabled, 8) image format with no strokes and all tick labels hidden.

Results

BOLD data-mining for Platygastroidea

Two hundred and one platygastrid and scelionid BINs were found to have intercontinental and island distributions (Table 2, Suppl. material 11). No cases were detected in the other platygastroid families. Of these, 140 were identified only to the family or subfamily level in BOLD, sometimes incorrectly. We identified all but one of these 140 BINs to a lower taxonomic level; 130 of them were identified to genus or lower. The dataset contains 27 genera (10 Platygastridae genera; 17 Scelionidae genera) (Table 2, Suppl. material 11). *Telenomus* (69 BINs) and *Platygaster* (35 BINs) are the most represented genera in their respective families. Canada (101 points) and Germany (90 points) are the most represented country level occurrence points in the platygastroid BIN dataset (Table 2, Suppl. material 11), likely biased by the existence of nationally directed barcoding initiatives.

The minimum BIN size was two (necessary for a geographic match) and the largest, a *Platygaster* species, contained 677 COI sequences. Most BINs (180 of 201) contained

Table 2. Summary of platygastroid and host BINs displaying intercontinental and island distributions in BOLD. Data on host associations were derived from summaries in Masner and Huggert (1989) and Austin and Field (1997).

Taxon	Intercontinental BINS	Host taxon	Intercontinental	Intercontinental
(parasitoid)	(parasitoid)		genera (host)	BINs (host)
Platygastridae				
Amblyaspis	5	Cecidomyiidae	43	476
Euxestonotus	2			
Leptacis	7			
Metaclisis	1			
Platygaster	35			
Synopeas	13			
Amitus	1	Aleyrodidae	13	35
Aphanomerus	1	Flatidae	2	4
		Ricaniidae	3	4
Allotropa	1	Pseudococcidae	13	34
Fidiobia	2	Chrysomelidae	45	94
		Curculionidae	92	210
Platygastrinae	4			
Scelionidae				
Anteris	1			
Aradophagus	2	Theridiidae	20	52
Baeoneurella	1	Lygaeidae	7	20
Baeus	4	Araneae		
Baryconus	1	Tettigoniidae	8	11
Calliscelio	1	Gryllidae	6	8
Dicroscelio	2			
Dyscritobaeus	1			
Gryon	6	Heteroptera		
Hadronotus	5	Lepidoptera		
Idris	9	Araneae		
Psix	1	Heteroptera		
Telenomus	69	Heteroptera Lepidoptera Diptera		
Trissolcus	11	Neuroptera Pentatomidae	21	27
Trissoicus Trimorus		Carabidae	48	
1rimorus Xenomerus	7	Carabidae	40	105
Scelionidae	1			
Scelioninae	T			
Teleasinae	2			
Telenominae	1			
reienominae	3			

fewer than 100 COI sequences (Fig. 1, Suppl. material 11). Intra-BIN maximum p-distances reported by BOLD ranged from 0.00% to 5.42% (Suppl. material 11). Most BINs (157 of 201) in the platygastroid dataset had an intra-BIN maximum p-distance of less than 2.50% (Suppl. material 11). P-distance to the nearest-neighbor BIN was reported from all the platygastroid BINs. These p-distances ranged from 0.99% to 17.86% (Suppl. material 11). Twenty-eight BINs had larger intra-BIN p-distances

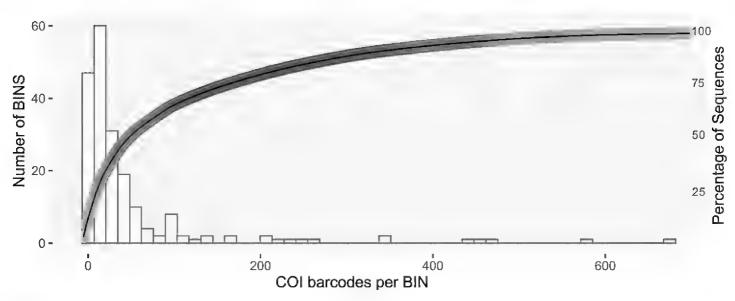


Figure 1. Pareto chart displaying the number of COI barcodes contained per BIN in the intercontinental and island platygastroid dataset.

than the p-distances to their nearest-neighbor BIN (Suppl. material 11). Fifty-five of the platygastroid BINs displayed exact COI matches across distant localities. These exact matches were discovered in *Amblyaspis* (2), *Amitus* (1), *Anteris* (1), *Aphanomerus* (1), *Dicroscelio* (1), *Euxestonotus* (2), *Fidiobia* (1), *Gryon* (2), *Idris* (3), *Leptacis* (2), *Platygaster* (9), *Psix* (1), *Synopeas* (5), *Telenomus* (18), *Trimorus* (1), *Trissolcus* (1), unidentified Platygastrinae (2), unidentified Scelioninae (1) and an unidentified Telenominae (1) (Suppl. material 11). Six BINs also included two exact intercontinental haplotype matches: *Euxestonotus* (1), *Gryon* (1), *Platygaster* (1), *Synopeas* (2) and *Telenomus* (1) (Suppl. material 11). An additional 28 BINs contained COI sequences that appeared to be exact matches, but were scored as inconclusive due to sequence length variation, precluding the most meaningful comparisons (Suppl. material 11).

In the total evidence Platygastroidea dataset, North America (248 connections), Europe (211 connections) and Asia (198 connections) were the most common connections (Fig. 2, Suppl. material 12). *Telenomus* and *Trissolcus* were the most represented scelionid genera across continents and islands. In Platygastridae, *Platygaster* and *Synopeas* were the most represented genera. The webs of geographic connection found in *Telenomus* and *Trissolcus* are more complex than those of *Platygaster* and *Synopeas* (Fig. 3, Suppl. materials 13, 14). For example, *Synopeas* and *Platygaster* lack any conclusive geographic data points in the Caribbean and Pacific Ocean and only one each in Africa. Europe and North America are the most connected continents in these genera, except for *Trissolcus* in which Asia and Europe are the most connected (Fig. 3, Suppl. materials 15, 16).

DNA sequence alignment and tree building

The intercontinental and island BIN dataset contains 9,874 platygastroid COI barcode sequences. The MAFFT alignment was 669 base pairs wide after trimming excessive data from the 3' end of some barcodes. The alignment contains some gap regions due to varying COI amino acid phenotypes present among Platygastroidea (Talamas

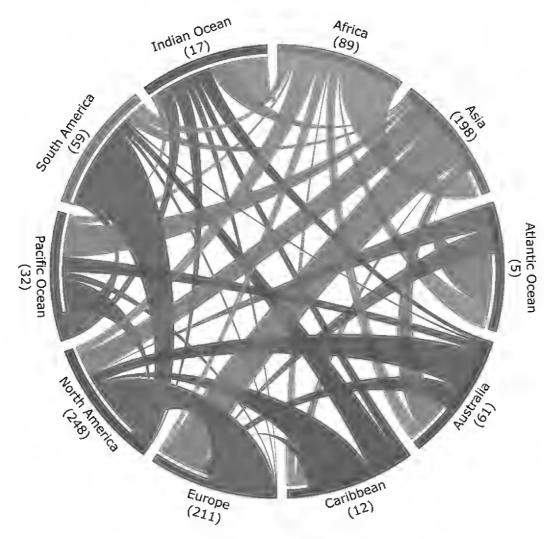


Figure 2. Circos plot displaying the relative contribution of continents and oceanic island groups to geographic connections in the combined platygastroid BOLD BIN, GBIF and literature dataset. Numbers in parentheses indicate the total number of connections to that geographic grouping.

et al. 2021). All positions with less than 95% site coverage were eliminated in the combined BIN p-distance neighbor-joining analysis; 520 positions were included in the final analysis. Terminal sequence clusters were collapsed and annotated to reflect their BIN assignment, revised or confirmed genus level identification and the number of sequences in that cluster (Fig. 4, Suppl. material 5). These terminal clusters corresponded unambiguously to their BIN assignment (i.e., they formed "monophyletic groups"), except in the case of *Telenomus* BOLD:AAU4881.

Identification and BOLD digital morphology

A total of 2,565 Platygastroidea BINs were evaluated for their identification accuracy using the specimen images provided by BOLD (Suppl. material 17). Nearly all these BINs were correctly identified to superfamily (12 were misidentified to order or family). Updated subfamily classification was provided for 2,551 platygastroid BINs (Suppl. material 17). A total of 2,209 BINs had images of sufficient quality to add genus level identifications. Sixty-four platygastroid genera were present among these BINs (Suppl. material 17), of which eight represent the first DNA sequence data for the genus in GenBank or BOLD: Euxestonotus, Gastrotrypes, Isocybus, Metaclisis, Parabaeus, Embioctonus, Styloteleia and Xenomerus.

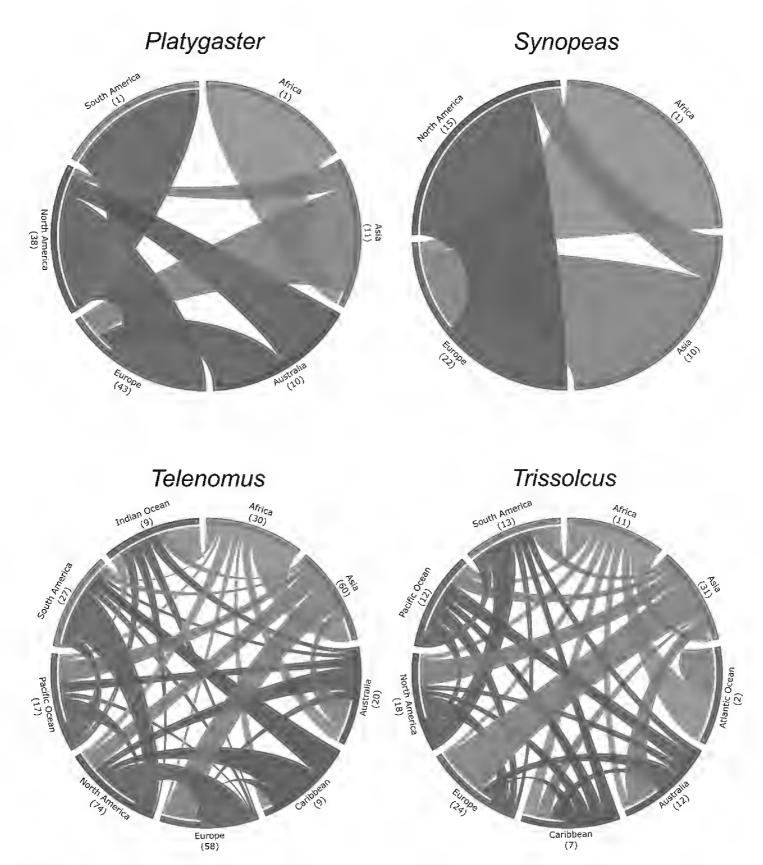


Figure 3. Circos plot displaying the relative contribution of continents and oceanic island groups to geographic connections in the combined *Platygaster*, *Synopeas*, *Telenomus* and *Trissolcus* BOLD BIN, GBIF and literature datasets. Numbers in parentheses indicate the total number of connections to that geographic grouping.

GBIF data-mining and literature search

GBIF and literature searches returned 130 intercontinental taxa (37 Platygastridae; 93 Scelionidae), with an overall discrepancy of plus 67 BINs (Table 3). The genera *Amblyaspis*, *Leptacis*, *Baeoneurella*, *Baryconus* and *Xenomerus* were present only in the BOLD BIN dataset (Table 3, Suppl. material 11). Conversely, the genera

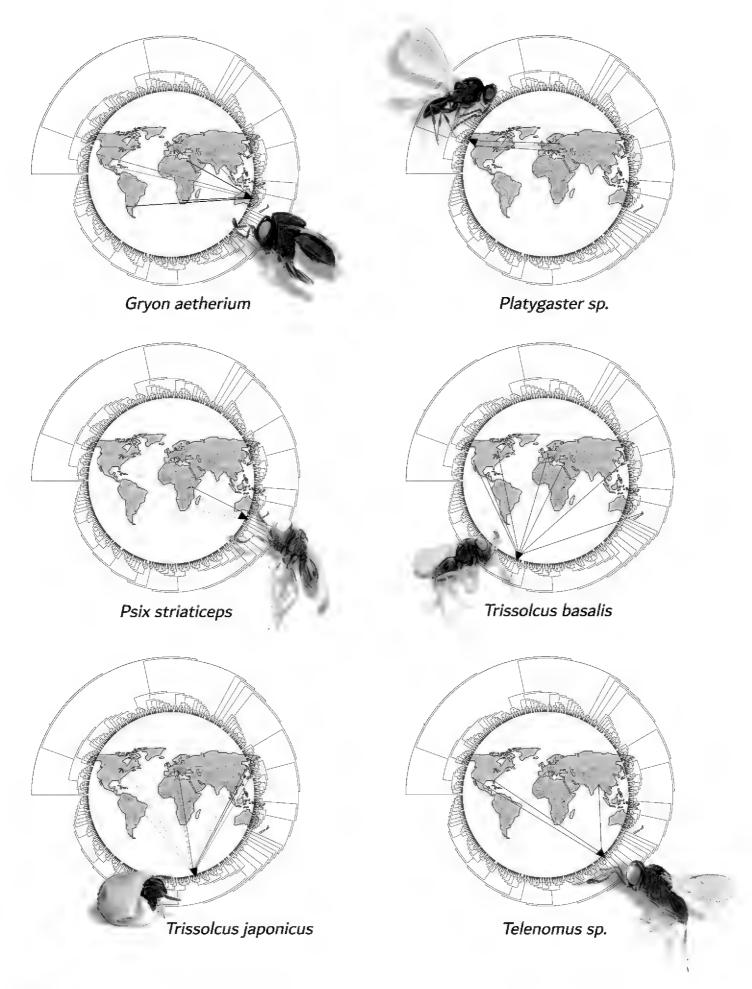


Figure 4. Circularized p-distance neighbor-joining tree of the intercontinental and island BOLD BIN dataset. The BOLD BINs containing *Gryon aetherium*, *Platygaster* sp. (BOLD:ACI8542), *Psix striaticeps*, *Trissolcus basalis*, *Tr. japonicus* and *Telenomus* sp. (BOLD:ACY0393) are highlighted by an enlarged terminal cluster. Lines emanating from these clusters show generalized geographic localities where the BIN was detected. Solid black lines indicate different COI haplotypes. Solid red or blue lines indicate exact COI haplotype matches across continents. Striped red and blue lines indicate multiple exact COI haplotype matches found at that generalized geographic locality.

Table 3. Comparison of total platygastroid intercontinental and island distributions present in different data sources.

Taxon	GBIF/Literature	BOLD BINs	Discrepancy
Platygastridae Total	37	72	+35 DNA
Allotropa	3	1	-2 DNA
Amblyaspis	0	5	+5 DNA
Amitus	4	1	-3 DNA
Aphanomerus	2	1	-1 DNA
Euxestonotus	1	2	+1 DNA
Fidiobia	2	2	-/-
Inostemma	1	0	-1 DNA
Leptacis	0	7	+7 DNA
Metaclisis	1	1	-/-
Platygaster	15	35	+20 DNA
Synopeas	7	13	+6 DNA
Tetrabaeus	1	0	-1 DNA
Scelionidae	93	129	+36 DNA
Anteris	1	1	-/-
Aradophagus	4	2	-2 DNA
Baeoneurella	0	1	+1 DNA
Baeus	2	4	+2 DNA
Baryconus	0	1	+1 DNA
Calliscelio	14	1	-13 DNA
Dicroscelio	1	2	+1 DNA
Duta	1	0	-1 DNA
Dyscritobaeus	3	1	-2 DNA
Gryon	4	6	+2 DNA
Hadronotus	4	5	+1 DNA
Idris	3	9	+6 DNA
Platyscelio	2	0	-2 DNA
Probaryconus	1	0	-1 DNA
Psix	3	1	-2 DNA
Scelio	1	0	-1 DNA
Telenomus	24	69	+45 DNA
Trimorus	1	7	+6 DNA
Trissolcus	24	11	-13 DNA
Xenomerus	0	1	+1 DNA

Inostemma, Tetrabaeus, Duta, Platyscelio, Probaryconus and Scelio were present only in the GBIF or literature datasets (Table 3, Suppl. material 6). In the process of analyzing the GBIF data, we encountered errors that were likely to be detected only by those with intimate knowledge of the group: Trissolcus japonicus (Ashmead) was listed as Gryon japonicum (Ashmead); records for Trissolcus cultratus (Mayr) were incomplete; Calliscelio elegans (Perkins) was listed as Caenoteleia elegans (Perkins); and Telenomus dalmanni (Ratzeburg) was misspelled as Telenomus dalmani. Notable name changes are that Trissolcus davatchii (Javahery) is now treated as a junior synonym of Tr. elasmuchae (Watanabe) and Tr. grandis (Thomson) is a junior synonym of Tr. belenus (Walker).

COI barcoding and identification of Platygastroids from the Jacksonville area

Talamas et al. (2017) provided names and images for species described from Jackson-ville with primary types in the National Museum of Natural History. This enabled identifications for taxa that have yet to be revised with modern standards, at least for species with distinctive morphology. For example, *Synopeas cynipsiphilum* (BOLD record SUPER036-23) has a conspicuous divide between the mesoscutum and mesoscutellum that make it easy to recognize. For many others, diagnostic characters were either unknown or too subtle for us to confidently make a determination of species without studying the taxon in detail. In some cases, we did not make a determination because the specimens we sequenced were not the same sex as the primary type. As these taxa are revised, we are certain that more matches will be made between our vouchers and primary types from the region. Of the specimens that yielded COI barcode data, we matched seven specimens to primary types, totalling six species (Table 4).

Forty-nine specimens were COI barcoded from Timucuan Ecological and Historic Preserve and Buck Island, Jacksonville, Florida (Table 4). Twenty-eight specimens had BOLD identification hits greater than 97% matches (Table 4), representing 25 BINs. Specimen vouchers FSCA 00094179 and FSCA 00094185, both identified as *Telenomus* sp., were 100% matches to a specimen from San Diego, California, USA in the BIN BOLD:ACY0393 (Table 4). This is an intercontinental *Telenomus* BIN identified from the Insecta scripting procedure (Fig. 4), now with geographic data points in California, Florida and Bangladesh.

COI barcoding of German specimens

Comparison of BOLD data to platygastrine specimens from the GBOL III barcoding initiative yielded 14 intercontinental BINs, representing 11 species in five genera (Amblyaspis, Euxestonotus, Leptacis, Platygaster and Synopeas). BOLD identified six species (seven BINs) only to family, two species (four BINs) to subfamily and three species (three BINs) with binomials. Of the three species identifications provided by BOLD, we verified two (Pl. demades and Pl. sagana) by comparison of voucher specimens to primary types, while one (Pl. tuberosula) was unverifiable. One more species (E. error) was unidentified in BOLD, but identifiable by our own examination. The remaining seven species were unidentifiable due to the superficial description impediment (Meier et al. 2022) in platygastrine taxonomy.

The distributions of two species (*Pl. demades* and putative *Pl. tuberosula*) can be explained by deliberate introductions for pest control on apple/pear and wheat, respectively. One species (*E. error*) is probably an unintentional introduction, moving with its host, the wheat midge *Sitodiplosis mosellana* (Géhin) (Echegaray et al. 2016). The biogeographic history of the remaining eight species could not be determined. It is possible that one of the unidentified *Platygaster* species (either BOLD:ACP1536 or BOLD:AAZ3286) is *Platygaster hiemalis* Forbes, deliberately introduced to New Zealand for control of the Hessian fly, *Mayetiola destructor* (Say) (Ferguson et al. 2007). However, the type material of *Pl. hiemalis* is unknown and the historical literature provides conflicting diagnoses.

BOLD data-mining for Insecta and Araneae

The R script recovered 15,391 Insecta BOLD BINs with intercontinental and island distributions (Suppl. material 7). Members of 23 Insecta orders were present in the dataset, with only Mecoptera, Notoptera (Mantophasmatodea and Grylloblattodea) and Zoraptera absent. Due to conflicting taxonomies present in BOLD, the family and genus representation numbers are close estimates of higher-level diversity. Orders with the most family- and genus-group diversity were Coleoptera (66 families; 560 genera), Lepidoptera (77 families; 1,984 genera), Diptera (82 families; 899 genera), Hymenoptera (62 families; 736 genera) and Hemiptera (64 families; 454 genera) (Table 5). Lepidoptera and Diptera contained the most BINs in the dataset (Table 5). The R script recovered 499 Araneae BOLD BINs with intercontinental and island distributions (Suppl. material 18). Members of 42 Araneae families were present, comprising 224 genera (Suppl. material 18).

We randomly selected 769 BINs from the Insecta dataset for cursory validation of the scripting process (Suppl. material 2). Validated BINs were examined in Blattodea (1), Coleoptera (50), Diptera (166), Ephemeroptera (5), Hemiptera (38), Hymenoptera (96), Lepidoptera (391), Neuroptera (1), Orthoptera (6), Plecoptera (1), Psocodea (1), Thysanoptera (6) and Trichoptera (7). No validation BINs were discovered to be geographic false positives upon the initial pass. However, four BINs (BOLD:AAC6546, BOLD:AAP8198, BOLD:AAE7880 and BOLD:AAD4954) were recalculated in BOLD during the intervening time period of data gathering, analysis and validation. These four BINs had the appearance of being geographic false positives, but they were confirmed to be accurate by comparison to the records present in the analyzed data files. Major taxonomic conflicts were present in Blattodea (1/1; 100%), Coleoptera (12/50; 24%), Diptera (44/166; 26%), Hemiptera (15/38; 39%), Hymenoptera (31/96; 32%), Lepidoptera (97/391; 25%), Neuroptera (1/1; 100%), Orthoptera (3/6; 50%) and Trichoptera (4/7; 57%) (Suppl. material 2). There were far fewer minor taxonomic conflicts (Lepidoptera = 19, Hymenoptera = 3, Hemiptera = 1, Diptera = 4) (Suppl. material 2). Twenty-five BINs from the Araneae dataset were randomly selected for validation of the scripting process (Suppl. material 19). Validated BINs were examined in Araneidae (1), Clubionidae (1), Gnaphosidae (1), Linyphiidae (10), Lycosidae (4), Pholcidae (1), Tetragnathidae (1), Theridiidae (4) and Thomisidae (2) (Suppl. material 19). No validation BINs were discovered to be geographic false positives upon the initial pass. Major taxonomic conflicts were present in Araneidae (1/1; 100%), Clubionidae (1/1; 100%), Linyphiidae (3/10; 30%), Lycosidae (1/4; 25%) and Thomisidae (1/2; 50%) (Suppl. material 19).

Greater than 80% of recovered Insecta BINs were present on two continents or islands (Fig. 5, Suppl. material 8), totalling 254 unique combinations of continent/island points (Suppl. material 9). Europe–North America (4,207 points), Asia–Europe (2,324 points), North America–South America (2,248 points), Asia–Australia (827 points) and Africa–Asia (665 points) were the five most common geographic combinations captured within Insecta BINs (Suppl. material 9). In total, North America (12,612 connections), Europe (11,402 connections) and Asia (8,728 connections)

Table 4. BOLD identification engine identifications for COI barcoded platygastroid specimens collected at Timucuan Ecological and Historic Preserve and Buck Island (Jacksonville Port Authority).

Processid	Sampleid	Morphological Identification	Topotype	% Match	Match Lowest Taxonomy	Match BIN
SUPER027-23	FSCA 00094159	Baeus	No	97.19	Scelionidae	BOLD:ACZ5774
SUPER008-23	FSCA 00094151	Baryconus floridanus	Yes	92.4	Scelionidae	BOLD:ABA5967
SUPER034-23	FSCA 00094155	Calotelea	No	100	Scelionidae	BOLD:AAN8024
SUPER043-23	FSCA 00093888	Calotelea bicolor	No	93.78	Scelionidae	BOLD:ADY8276
SUPER047-23	FSCA 00091193	Hadronotus bicolor	No	99.36	Gryon bicolor	BOLD:AAN8046
SUPER048-23	FSCA 00090993	Hadronotus bicolor	No	98.84	Gryon bicolor	BOLD:AAN8046
SUPER049-23	FSCA 00091003	Hadronotus bicolor	No	99.36	Gryon bicolor	BOLD:AAN8046
SUPER002-23	FSCA 00090995	Hadronotus carinatifrons	No	99.5	Hadronotus carinatifrons	BOLD:AET1244
SUPER042-23	FSCA 00093865	Hadronotus chelinideae	No	98.87	Gryon chelinideae	BOLD:ACN3082
SUPER040-23	FSCA 00097242	Inostemma	No	98.79	Platygastridae	BOLD:ACT8287
SUPER045-23	FSCA 00093946	Leptacis longipes	Yes	93.63	Leptacis	BOLD:ABV2678
SUPER044-23	FSCA 00093928	Leptacis puncticeps	Yes	97.47	Platygastridae	BOLD:AEE0956
SUPER001-23	FSCA 00091067	Metaclisis	No	92.26	Platygastridae	BOLD:AEC9177
SUPER037-23	FSCA 00097245	Metanopedias brunneipes	Yes	98.77	Platygastridae	BOLD:ABY3815
SUPER028-23	FSCA 00094161	Phanuromyia	No	91.2	Scelionidae	BOLD:ACJ7306
SUPER033-23	FSCA 00094146	Phanuromyia	No	99.84	<i>Telenomus</i> autumnalis (unavailable name)	BOLD:ACM1917
SUPER004-23	FSCA 00094172	Phanuromyia	No	89.62	Scelionidae	BOLD:AEN8490
SUPER005-23	FSCA 00094176	Phanuromyia	No	86.37	Scelionidae	BOLD:ADH6867
SUPER006-23	FSCA 00094152	Phanuromyia	No	86.9	Scelionidae	BOLD:ADH6867
SUPER007-23	FSCA 00094154	Phanuromyia	No	98.72	Telenomus	BOLD:AAN8100
SUPER022-23	FSCA 00095852	Platygaster	No	96.54	Platygastridae	BOLD:AAN8090
SUPER039-23	FSCA 00097243	Platygaster	No	87.64	Platygastridae	BOLD:ADI9080
SUPER010-23	FSCA 00094167	Scelio floridanus	Yes	98.74	Scelionidae	BOLD:ACA7140

Processid	Sampleid	Morphological Identification	Topotype	% Match	Match Lowest Taxonomy	Match BIN
SUPER029-23	FSCA 00094138	Scelio floridanus	Yes	98.89	Scelionidae	BOLD:AEY5850
SUPER009-23	FSCA 00094175	Scelio incertus	No	99.53	Scelionidae	BOLD:ACA7140
SUPER041-23	FSCA 00093881	Scelio opacus	No	95.27	Scelionidae	BOLD:ACT6721
SUPER035-23	FSCA 00093874	Scelio pumilis	No	99.81	Scelio	BOLD:ACA7141
SUPER003-23	FSCA 00095771	Synopeas	No	93.94	Platygastridae	BOLD:ADH8704
SUPER038-23	FSCA 00095854	Synopeas	No	99.53	Platygastridae	BOLD:AAY6787
SUPER017-23	FSCA 00094197	Synopeas	No	93.38	Platygastridae	BOLD:ACM5719
SUPER018-23	FSCA 00095010	Synopeas	No	94.16	Platygastridae	BOLD:ADH9879
SUPER019-23	FSCA 00095011	Synopeas	No	93.62	Platygastridae	BOLD:ADH9879
SUPER020-23	FSCA 00095851	Synopeas	No	99.84	Synopeas	BOLD:AEP1939
SUPER021-23	FSCA 00097239	Synopeas	No	99.68	Platygastridae	BOLD:AEP1939
SUPER036-23	FSCA 00097487	Synopeas cynipsiphilum	Yes	99.04	Synopeas	BOLD:ADX3415
SUPER011-23	FSCA 00094179	Telenomus	No	100	Scelionidae	BOLD:ACY0393
SUPER012-23	FSCA 00094185	Telenomus	No	100	Scelionidae	BOLD:ACY0393
SUPER013-23	FSCA 00094149	Telenomus	No	100	Scelionidae	BOLD:ACV4748
SUPER014-23	FSCA 00094165	Telenomus	No	100	Scelionidae	BOLD:AEO7335
SUPER015-23	FSCA 00094156	Telenomus	No	100	Telenomus	BOLD:AAN8031
SUPER016-23	FSCA 00094137	Telenomus	No	100	Telenomus	BOLD:ABW3189
SUPER032-23	FSCA 00094153	Telenomus	No	100	Scelionidae	BOLD:ACI3554
SUPER046-23	FSCA 00093915	Telenomus	No	99.35	<i>Telenomus</i> sp. SL017	BOLD:AEI6588
SUPER023-23	FSCA 00094140	Telenomus	No	97.11	Scelionidae	BOLD:ACX8754
SUPER024-23	FSCA 00094150	Telenomus	No	93.81	Scelionidae	BOLD:ADY7126
SUPER025-23	FSCA 00094139	Telenomus	No	99.68	Telenomus	BOLD:ABY2759
SUPER026-23	FSCA 00094173	Telenomus	No	93.84	Telenomus podisi	BOLD:ADK2938
SUPER030-23	FSCA 00094249	Trimorus	No	94.94	Scelionidae	BOLD:AEJ7657
SUPER031-23	FSCA 00094136	Trimorus	No	99.52	Trimorus	BOLD:ABV9390

Table 5. Taxonomic summary of Insecta BINs displaying geographic distributions spanning continents and islands.

Order	Families	Genera	BINs
Archaeognatha	1	1	1
Zygentoma	1	3	3
Odonata	8	51	91
Ephemeroptera	7	18	37
Dermaptera	4	7	11
Plecoptera	4	8	10
Orthoptera	6	44	62
Embioptera	2	3	5
Phasmatodea	2	4	4
Mantodea	1	5	7
Blattodea	7	31	60
Psocodea	21	30	107
Thysanoptera	3	29	86
Hemiptera	64	454	924
Hymenoptera	62	736	3,056
Raphidioptera	1	1	1
Neuroptera	5	15	43
Strepsiptera	2	2	2
Coleoptera	66	560	1,121
Trichoptera	17	47	126
Lepidoptera	77	1,984	5,336
Siphonaptera	3	6	12
Diptera	82	899	4,286
Total: 23	446	4,938	15,391

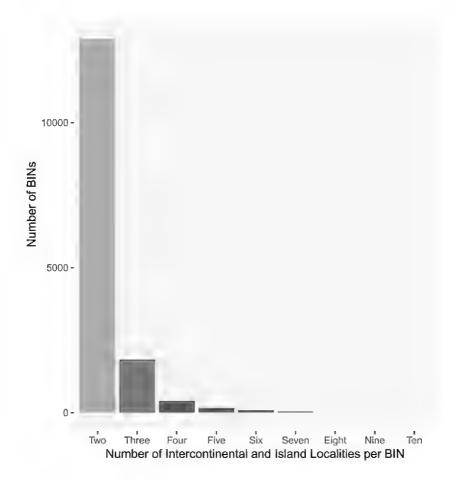


Figure 5. Histogram displaying the percentage of Insecta BINs with a given number of continent and island data points.

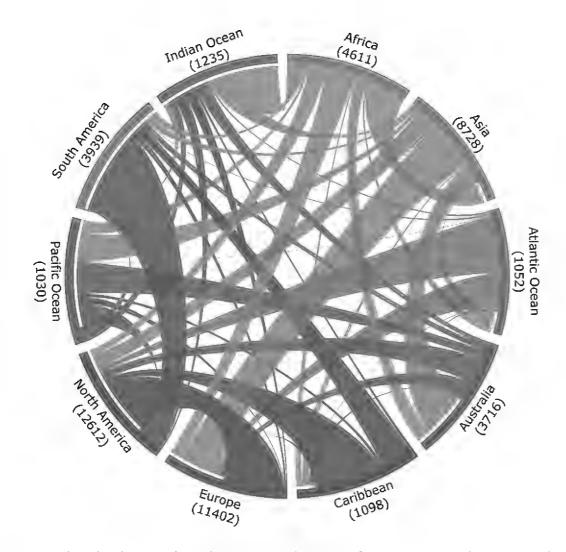


Figure 6. Circos plot displaying the relative contribution of continents and oceanic island groups to geographic connections in the Insecta BOLD BIN dataset. The single data point for Antarctica was eliminated from this visualization. Numbers in parentheses indicate the total number of connections to that geographic grouping.

were the most connected geographic categories (Fig. 6, Suppl. material 10). Europe—North America (5,563 connections), Europe—Asia (3,549 connections), North America—South America (2,718 connections), North America—Asia (1,520 connections), Africa—Asia (1,458 connections) and Australia—Asia (1,345 connections) were the most common connections in Insecta BINs (Fig. 6, Suppl. material 10).

Discussion

Lessons from Platygastroidea

Our BOLD data-mining approach confirmed several well-characterized cases of parasitoid range expansion in *Tr. basalis, Tr. japonicus, Tr. hyalinipennis, Te. remus, G. aetherium, Ps. striaticeps* and *Pl. demades.* Therefore, the geographic distribution patterns found in the platygastroid dataset are generally considered credible even when lacking any directionality. The effort of COI barcoding topotypical specimens can be helpful for determining directionality, particularly if the specimens match primary types described a long time ago. Antiquity of specimens does not preclude the possibility that they were adventive at the time of collection, but it gives, at minimum, a historical perspective.

Exact COI barcode matches from geographically disparate populations might be the most conclusive evidence of a new adventive population within our framework. However, even among the validated cases mentioned above, only *Te. remus*, *G. aetheri-um* and *Ps. striaticeps* were scored as exact long-distance matches. *Trissolcus japonicus* and *Tr. basalis* both have the appearance of exact intercontinental matches, but were scored inconclusive due to sequence length variation. *Trissolcus hyalinipennis* and *Pl. demades* have no evidence for exact intercontinental matches in our dataset. Specimens identified as *Pl. demades* are divided into five BOLD BINS, two of which contain populations introduced into Canada and the USA (Mason et al. 2017). These Nearctic *Pl. demades* BINs were not captured by our method and show that the expectation of exact matches may be unnecessary when inferring range expansion, although it does lend additional confidence. The BIN calculations still captured relevant information in these cases even though additional geographic data points were present in neighboring BINs.

A majority of the intercontinental platygastroid BINs were unidentified below the family level at the beginning of this study, affording our group a "clean" taxonomic slate on which to analyze and interpret these results. Alternatively, the identifications for many of the validated intercontinental Insecta BINs were conflicted, which confounds interpretation of the data. Conflicting taxonomies present in BOLD BINs complicated our ability to extract and summarize higher-level taxonomic data from the Insecta dataset. Even if these taxonomic conflicts can be rectified or understood on a case-by-case basis by expert systematists, that database problem is likely to persist in future analyses. We advocate that experts use our baseline dataset to closely examine the intercontinental BINs in their group of interest and make informed judgements about their veracity.

Many of the BOLD BIN criticisms levelled by Meier et al. (2022) are applicable to our approach. We found that BOLD BIN recalculations affected our study, once again demonstrating their instability. A few of our validation BINs were missing when they were queried back to BOLD for checking, having been recalculated between the time of database mining and data analysis. This feature of BOLD BINs will certainly complicate repetition of our analyses in the future. For better or worse, we must rely on BINs calculated database-wide for our proposed method because they are tied to the specimen metadata in an efficient way for mining. To further verify our relatively small (nearly 10,000 COI barcodes) platygastroid dataset, the sequences could be aligned, phylogenetically analyzed and those results used to provide de novo mOTUs by varying methods with more public documentation than RESL (Ratnasingham and Hebert 2013). However, this smaller sampling of barcodes would influence mOTU calculations. The most rigorous results would be obtained by analyzing all available Platygastroidea data in BOLD, comprising well over 140,000 COI barcodes and growing. Such large analyses would firmly move our method into the realm of bioinformaticians and supercomputing, rather than being repeatable by scientists with less capability for big data. We consider it a major strength that our approach can be performed on an internet-connected, standard desktop computer with freely-available statistical software.

Our case study of Platygastrinae using GBOL specimens indicated that BINs overestimated "species richness" and we reiterate that the BINs in the Insecta and Platygastroidea dataset do not necessarily equate to species. Results for poorly-known or hyperdiverse insect groups must be interpreted with caution.

Natural or adventive distributions in Platygastroidea?

Platygastroid wasps are one of the most dominant flying insect groups worldwide, with a high rate of geographically structured community turnover and high taxonomic neglect, further complicating faunistic studies (Srivathsan et al. 2023). Srivathsan et al. (2023) discovered 44 platygastroid mOTUs in multiple sampling sites. They also reported that usually less than 3% (1–9% within a given insect family) of their mOTUs in the top 20 most dominant insect families were found at multiple sites. About five members of our platygastroid BIN dataset display geographic ranges which may be "false positives" based on our intentions. For example, BINs shared between the Republic of Georgia and Iran or Egypt and Saudi Arabia were scored as intercontinental even though these countries are in close geographic proximity. Conservatively, we detected 195 platygastroid BINs comprising specimens with vast geographic ranges. As of February 2023, BOLD analytics has calculated 11,468 Platygastroidea BINs. From our study, approximately 1.7% of available platygastroid BINs display this striking distribution pattern.

Determining whether these distributions are natural or adventive for most of the platygastroid BINs is difficult pending taxonomic revisions and follow-up research. Gilligan et al. (2020) suggested that a species association with Beringia supports hypothetically natural Holarctic distributions in Tortricidae (Lepidoptera), while also providing a good list of expectations for Holarctic species versus recent introductions. For truly Holarctic organisms, expectations include: 1) no direct evidence of introduction, 2) association with native hosts, 3) initial reports from inland areas, 4) lack of recent range expansion and 5) presence in the Arctic biogeographic region (Gilligan et al. 2020). These expectations are a useful framework for assessing many of the intercontinental platygastroid BINs present in Canada, Europe and northeast Asia.

Many Platygastroidea distributions in the BOLD dataset were from the Southern Hemisphere, between the Northern and Southern Tropics or island localities, precluding the need to consider a naturally Holarctic distribution as an explanation for the pattern. We think those cases are best considered introductions mediated by human activity. However, in some *Platygaster* and *Telenomus* BINs, the locality data imply enormous geographic ranges across the entirety of Canada, northern and central Europe, northeastern Asia and other spurious localities. For example, *Telenomus* sp. (BOLD:AAV1142; 461 public barcodes) has occurrences across Canada including Nunavut in the north, south to desert regions of eastern California and eastern Europe. One unidentified platygastrine (BOLD:ABW3192; 37 public barcodes with several exact matches) has occurrences in eastern and western Canada, Germany, the Russian Far East, South Africa and California. These geographic ranges encompass several

climates and biomes, showing the apparent ability of the wasps to tolerate dramatically different environmental conditions for at least a short period, considering that species that fail to establish would have to persist long enough to be collected.

Historically, the Palearctic and Nearctic Regions have been regarded as separate by platygastroid taxonomists. Early European authors rarely made comparisons to the fauna of neighboring countries, let alone distant continents. Likewise, early American hymenopterists often treated the Nearctic fauna as unique. This approach contrasts with that of early American lepidopterists, who tended to misidentify Nearctic species as similar-looking European species (Gilligan et al. 2020). The discrepancy may be explained by the availability of detailed keys and illustrations for Lepidoptera in the 19th century, while descriptions of Platygastroidea were generally short and vague.

Contrary to the assumptions of the past, the results of our study suggest that some platygastroid genera, such as *Platygaster*, include many naturally Holarctic species as well as human-mediated introductions. Landry et al. (2013) came to a similar conclusion for Lepidoptera, with the added benefit of host plant data to help distinguish natural from anthropogenic distributions. It is difficult to make such determinations for Platygastrinae, as little is known of their host repertoire and Cecidomyiidae is itself a dark taxon. However, our results also indicate a high number of intercontinental cecidomyiid BINs, which matches well with the parasitoid distributions.

Constraints due to a lack of data are a consistent theme throughout platygastroid taxonomy, especially when compared with better-studied groups of insects. Our method offers a path to gather and interpret the available data, albeit with limitations. For example, the Nearctic and western Palearctic were remarkably well sampled, allowing for more detailed examination of distribution patterns. On the other hand, the Pacific Islands and Caribbean yielded no *Platygaster* or *Synopeas* records. This likely reflects reality in the Pacific Islands but is a result of under sampling in the Caribbean, a distinction which cannot be made by our method alone. Ashmead (1900) recorded 29 species of platygastrine wasps from St. Vincent and Grenada, while the only platygastrine in Hawaii is considered an accidental introduction (Drake 1969).

Digital morphology in BOLD

Specimen images in BOLD allowed us to provide a list of genus level identifications for about one fifth of all platygastroid BOLD BINs. This has just begun the process of overcoming taxonomic impediments in the group and the database more broadly, as many thousands of BINs remain to be examined and identified. Platygastroid wasps are generally small insects (0.5 to 10 mm), making species level characters difficult to assess without proper microscopy and high-resolution images. Regardless, the image quality and habitus views in BOLD were generally sufficient to identify BINs to genus. We encourage systematists to examine BIN images in their group of expertise to see if this process can be repeated for other under-studied insect families. Given that we discovered several BINs which contained genera lacking any other DNA sequence data, is it likely that more such cases remain to be found.

Data presented here suggest that taxonomic revisions of platygastroids should be targeted at the global level as much as possible, even if there are feasibility concerns. A consideration of data from across the world will likely be necessary for the accurate and precise description of some sections of platygastrid and scelionid biodiversity. The BIN database should be preemptively searched to quickly quantify diversity present in an area and inform the taxonomic approach. Our genus level identification of BINS has already facilitated one such study. Melotto et al. (2023) described a new species, *Synopeas maximum* Awad & Talamas, which parasitizes an emerging pest of soybean. Given that soybean is a cosmopolitan crop, it was a possibility that this parasitoid was adventive. A phylogenetic analysis of *Synopeas* BINs enabled them to determine that the closest relatives of *S. maximum* are from North America, suggesting that it was not adventive. Furthermore, specimen images in BOLD allowed them to assess if certain morphological characters corresponded to a monophyletic species group.

On another research track, the molecular evolution of COI barcodes across Animalia was evaluated by Pentisaari et al. (2016), demonstrating that parasitic groups had many convergent amino acid variations. Several COI barcode amino acid phenotypes have been noted in Platygastroidea and some appear informative at the genus level (Talamas et al. 2021). Increased BOLD resolution for Platygastroidea genera could allow for new analyses of these patterns for the superfamily (Chen et al. 2021).

Implications for biological control programs

These analyses highlight the urgent need for more detailed and comprehensive approaches (Talamas et al. 2021) when identifying biological control agents, whether classical or augmentative. This is especially the case for platygastroid egg parasitoids; they are small, cryptic and their biodiversity dwarfs what has been adequately described. They also attack small, cryptic and poorly-described insect life stages. COI barcoding of proposed classical biological control agents must occur immediately at program outset. New data can then be quickly assessed as distinct or not present in BINs calculated from other non-native areas. Putatively "native" communities of parasitoids being evaluated for use as augmentative biological control agents should be similarly treated. Our results and those of Srivathsan et al. (2023) demonstrate the significant likelihood of unintended and undocumented platygastroid introductions.

Insecta and Araneae

Approximately 84% (12,876/15,391) of the recovered intercontinental and island Insecta BINs were detected across two geographic categories. When these geographic categories are contiguous or adjacent, they are the most likely to be 'false positives' based on our data-mining approach. For example, BINs present in lowland rainforest habitats of both Costa Rica and Colombia were scored as intercontinental even though these are probably natural distributions (North America/South America; 2,248 BINs). Indeed, there are many such cases in the dataset, especially among Neotropical

Lepidoptera BINs. In the Palearctic, Europe and Asia (2,324 BINs) were connected at a similar magnitude. BINs detected across contiguous landmasses warrant additional scrutiny by taxonomic experts to determine their status as adventive or natural distributions. Just over 2,500 Insecta BINs were detected from three or more continents or island chains. This set of BINs contains insect species which appear to be truly successful global invaders. Our results were intuitive for insect BOLD BINs with the most widespread geographic data; these included species long associated with human activity. For example, *Ctenocephalides felis* (cat flea; BOLD:AAY6332), *Aedes aegypti* (yellow fever mosquito; BOLD:AEI9358), *Culex quinquefasciatus* (southern house mosquito; BOLD:AAA4751) and *Aphis gossypii* (cotton aphid; BOLD:AAA3070) were recovered in the analysis with 9 or 10 intercontinental and island data points.

The highly structured global sampling of flying insect communities undertaken by Srivathsan et al. (2023) provides some meaningful context for our results. In that study, greater than 97% of mOTUs from the most dominant flying insect families were sampled only at a single site, suggesting massive community turnover between sites (Srivathsan et al. 2023). Our BIN dataset, which notably was not designed for statistical testing a priori nor sorted by biological traits, suggests that about 3.15% of the BOLD Insecta BINs are distributed across continents and islands (489,156 Insecta BINs as of September 2023). Simpson et al. (2021) considered 3,747 insects and 58 spiders to be adventive in the continental United States. That dataset serves as a valuable baseline of verified introductions for comparison to the BOLD BINs provided herein. We found 12,612 intercontinental Insecta BINs with a distribution that included North America, indicating a large discrepancy between these methods. Our larger number may be an artifact of the data-mining approach, as mentioned previously, but may also reflect undetected introductions. Rectifying these datasets is a herculean task, given their size and the taxonomic expertise needed. However, given the magnitude of the agricultural, environmental and economic consequences of invasive species, this should be a research priority for biosecurity experts, bioinformaticians and systematists.

Regulatory and biosecurity applications

Biosecurity practices entail anticipatory risk assessment and preparedness, methods of surveillance, emergency management and policy enforcement (Barker and Francis 2021). This dataset has potential applications for risk assessment and surveillance. Our approach sought to use large geographic spans in BINs with the goal of identifying putatively adventive platygastroids. Small adjustments to the data-mining and analysis methods could be made to focus on administrative borders instead. BOLD data have already been used to inventory fauna at the country level (Geiger et al. 2016; Hebert et al. 2016), making new BIN additions to Canada and Germany straightforward to detect.

Emerging infectious disease surveillance programs have implemented several automated, internet-based data-mining approaches for intelligence gathering (Stevens 2021). Similarly, automation and scheduled repetition of a modified version of our analysis could provide information supporting risk assessment and invasion prepared-

ness as BINs accumulate in new geographic areas. Detection at the earliest stages of invasion, followed by rapid response, provides the best economic and environmental outcomes. This proposed method of biosecurity surveillance will probably not be timely enough to meet early detection criteria; once new data points are detected in an area, the proverbial cat is already out of the bag. Agencies also rely on in-hand specimens for diagnosis of regulated species and are unlikely to take a decentralized BIN record as definitive evidence of new introductions. However, this may be a situation analogous to several cases of verified arthropod introductions that were first noticed or tracked as records in iNaturalist and BugGuide (Iwane 2018; Halbert et al. 2020; USDA 2021; Hayden et al. 2022; Chuang et al. 2023; iNaturalist 2023; VanDyk 2023).

Further scrutinizing the Insecta BINs with consideration for specimen spatiotemporal data might also inform pathway analyses for species moving via global trade, weather phenomena or animal migration events. Data from the Jacksonville area uncovered an intercontinental *Telenomus* species, with matching specimens collected in 2014 and 2015 from coastal areas of Bangladesh and California. Relevant agencies could have been alerted to the risk of this new introduction, possibly centered around international seaports-of-entry, eight years prior if the available data were scanned systematically. Thus, nearly a decade of potential research progress on this unidentified, globally-mobile *Telenomus* went unrealized. Cases like these might be valuable input for pathway models or agent-based models of long-distance insect dispersal. Detailed examination of the Insecta BIN dataset should reveal similar cases for groups with a widely-variable range of life history traits, dispersal potentials and introduction histories or modalities.

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Country to continent and island group assignments

Authors: Matthew R. Moore, Elijah J. Talamas, Jonathan S. Bremer, Natalie McGathey, James C. Fulton, Zachary Lahey, Jessica Awad, Cheryl G. Roberts, Lynn A. Combee Data type: xlsx

Explanation note: File detailing country and island continent assignments.

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Randomized BOLD BINs for validation of the Insecta dataset

Authors: Matthew R. Moore, Elijah J. Talamas, Jonathan S. Bremer, Natalie McGathey, James C. Fulton, Zachary Lahey, Jessica Awad, Cheryl G. Roberts, Lynn A. Combee Data type: xlsx

Explanation note: Table detailing which Insecta BINs were validated by manual examination.

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Link: https://doi.org/10.3897/neobiota.88.106326.suppl2

Supplementary material 3

Intercontinental and island Platygastroidea COI dataset alignment

Authors: Matthew R. Moore, Elijah J. Talamas, Jonathan S. Bremer, Natalie McGathey, James C. Fulton, Zachary Lahey, Jessica Awad, Cheryl G. Roberts, Lynn A. Combee Data type: fas

Explanation note: DNA alignment of COI barcodes from intercontinental and island platygastroids.

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Platygastroidea COI dataset NJ tree.tre

Authors: Matthew R. Moore, Elijah J. Talamas, Jonathan S. Bremer, Natalie McGathey, James C. Fulton, Zachary Lahey, Jessica Awad, Cheryl G. Roberts, Lynn A. Combee Data type: tre

Explanation note: P-distance NJ tree of platygastroid COI barcodes.

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Link: https://doi.org/10.3897/neobiota.88.106326.suppl4

Supplementary material 5

Platygastroidea COI dataset NJ tree annotated FIGTREE

Authors: Matthew R. Moore, Elijah J. Talamas, Jonathan S. Bremer, Natalie McGathey, James C. Fulton, Zachary Lahey, Jessica Awad, Cheryl G. Roberts, Lynn A. Combee Data type: tre

Explanation note: FigTree file of annotated p-distance NJ tree Newick tree.

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Intercontinental and island records for targeted Platygastroidea in GBIF and the literature

Authors: Matthew R. Moore, Elijah J. Talamas, Jonathan S. Bremer, Natalie McGathey, James C. Fulton, Zachary Lahey, Jessica Awad, Cheryl G. Roberts, Lynn A. Combee Data type: xlsx

Explanation note: Data summary for platygastroid taxa with GBIF and literature Records. Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.88.106326.suppl6

Supplementary material 7

List of intercontinental and island Insecta BINs with identification metadata

Authors: Matthew R. Moore, Elijah J. Talamas, Jonathan S. Bremer, Natalie McGathey, James C. Fulton, Zachary Lahey, Jessica Awad, Cheryl G. Roberts, Lynn A. Combee Data type: xlsx

Explanation note: List of Insecta BINs recovered by the scripting procedure as intercontiental or island hits, BINs listed under Identification Remarks.

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Number of distinct continent or island groupings recovered per Insecta BIN

Authors: Matthew R. Moore, Elijah J. Talamas, Jonathan S. Bremer, Natalie McGathey, James C. Fulton, Zachary Lahey, Jessica Awad, Cheryl G. Roberts, Lynn A. Combee Data type: csv

Explanation note: Table displaying number of continent and island hits per Insecta BIN.

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Link: https://doi.org/10.3897/neobiota.88.106326.suppl8

Supplementary material 9

Unique continent and island hit combinations in Insecta dataset

Authors: Matthew R. Moore, Elijah J. Talamas, Jonathan S. Bremer, Natalie McGathey, James C. Fulton, Zachary Lahey, Jessica Awad, Cheryl G. Roberts, Lynn A. Combee Data type: csv

Explanation note: Table showing frequencies of geographic combinations in the Insecta BIN dataset.

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Pairwise geographic hit comparisons for the Insecta BIN dataset

Authors: Matthew R. Moore, Elijah J. Talamas, Jonathan S. Bremer, Natalie McGathey, James C. Fulton, Zachary Lahey, Jessica Awad, Cheryl G. Roberts, Lynn A. Combee Data type: xlsx

Explanation note: Pairwise matrix used to generate Circos plot in Figure 1.

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Link: https://doi.org/10.3897/neobiota.88.106326.suppl10

Supplementary material II

Summary of intercontinental and island Platygastroidea BINs

Authors: Matthew R. Moore, Elijah J. Talamas, Jonathan S. Bremer, Natalie McGathey, James C. Fulton, Zachary Lahey, Jessica Awad, Cheryl G. Roberts, Lynn A. Combee Data type: xlsx

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Link: https://doi.org/10.3897/neobiota.88.106326.suppl11

Supplementary material 12

Pairwise geographic hit comparisons for the Platygastroidea BIN, GBIF, and literature dataset

Authors: Matthew R. Moore, Elijah J. Talamas, Jonathan S. Bremer, Natalie McGathey, James C. Fulton, Zachary Lahey, Jessica Awad, Cheryl G. Roberts, Lynn A. Combee Data type: xlsx

Explanation note: Matrix used to generate Circos plot in Figure 4.

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Pairwise geographic hit comparisons for the Platygaster BIN, GBIF, and literature dataset

Authors: Matthew R. Moore, Elijah J. Talamas, Jonathan S. Bremer, Natalie McGathey, James C. Fulton, Zachary Lahey, Jessica Awad, Cheryl G. Roberts, Lynn A. Combee Data type: xlsx

Explanation note: Matrix used to generate Circos plot in Figure 5.

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Link: https://doi.org/10.3897/neobiota.88.106326.suppl13

Supplementary material 14

Pairwise geographic hit comparisons for the Synopeas BIN, GBIF, and literature dataset

Authors: Matthew R. Moore, Elijah J. Talamas, Jonathan S. Bremer, Natalie McGathey, James C. Fulton, Zachary Lahey, Jessica Awad, Cheryl G. Roberts, Lynn A. Combee Data type: xlsx

Explanation note: Matrix used to generate Circos plot in Figure 5.

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Pairwise geographic hit comparisons for the Telenomus BIN, GBIF, and literature dataset

Authors: Matthew R. Moore, Elijah J. Talamas, Jonathan S. Bremer, Natalie McGathey, James C. Fulton, Zachary Lahey, Jessica Awad, Cheryl G. Roberts, Lynn A. Combee Data type: xlsx

Explanation note: Matrix used to generate Circos plot in Figure 5.

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Link: https://doi.org/10.3897/neobiota.88.106326.suppl15

Supplementary material 16

Pairwise geographic hit comparisons for the Trissolcus BIN, GBIF, and literature dataset

Authors: Matthew R. Moore, Elijah J. Talamas, Jonathan S. Bremer, Natalie McGathey, James C. Fulton, Zachary Lahey, Jessica Awad, Cheryl G. Roberts, Lynn A. Combee Data type: xlsx

Explanation note: Matrix used to generate Circos plot in Figure 5.

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Platygastroidea BIN identifications using digital morphology infrastructure

Authors: Matthew R. Moore, Elijah J. Talamas, Jonathan S. Bremer, Natalie McGathey, James C. Fulton, Zachary Lahey, Jessica Awad, Cheryl G. Roberts, Lynn A. Combee Data type: xlsx

Explanation note: Table of wasp identifications provided to BOLD by using existing digital morphology infrastructure.

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Link: https://doi.org/10.3897/neobiota.88.106326.suppl17

Supplementary material 18

List of intercontinental and island Araneae BINs with identification metadata

Authors: Matthew R. Moore, Elijah J. Talamas, Jonathan S. Bremer, Natalie McGathey, James C. Fulton, Zachary Lahey, Jessica Awad, Cheryl G. Roberts, Lynn A. Combee Data type: csv

Explanation note: List of BOLD metadata for intercontinental and island Araneae identified using the scripting procedure. BINs are under Identification Remarks.

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Randomized BOLD BINs for validation of the Araneae dataset

Authors: Matthew R. Moore, Elijah J. Talamas, Jonathan S. Bremer, Natalie McGathey, James C. Fulton, Zachary Lahey, Jessica Awad, Cheryl G. Roberts, Lynn A. Combee Data type: xlsx

Explanation note: Table of Araneae BINs manually examined for validation of Araneae BOLD scripting procedure.

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